THE MEIOTIC CYTOKINESIS OF NELUMBO

CLIFFORD H. FARR

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The division of the cell is a phase of cytology which has proved to have a wide application to other branches of biological science. The division of the nucleus through the phenomena of karyokinesis and other chromatin behaviors has been found to be of direct importance to the subject of genetics. The partitioning of the cell, or cytokinesis, has on the other hand thrown light on the dynamics of the cell and cell physiology and is also closely related to growth, a very important phase of physiological investigation. The recognition of the fact that growth embraces not only cell enlargement, but cell division and cell differentiation, and also, in the multicellular organism, intercellular stresses and strains, warrants a renewed attack upon the field of cytokinesis. I. W. Bailey (1–5) has recently been making an extensive study of cell-plate formation in the cambium, and has shown very clearly how cell-plate formation may be adapted to the longitudinal division. of very much elongated cells. Another line of investigation of cytokinesis in plants has been the establishment of the existence of cell division without cell plates but by a furrowing process in the formation of the microspores of certain Angiosperms. This was demonstrated by the writer first in Nicotiana, Primula, Helianthus, Ambrosia, Tropaeolum, and Chrysanthemum (6), and later in Magnolia (7) and Sisyrinchium, a monocotyledon (8). Mrs. W. K. Farr has also found the same procedure in Cobaea (9).

While the writer's first paper (6) was in press, Tahara (20) published a paper entitled "Cytological Studies on Chrysanthemum" in which he states that

> At the end of the meiotic nuclear division, the new partition cell walls appear in the form of protuberances in the inner surface of the cell wall of the pollen mother cells. These protuberances proceed centripetally and constrict the pollen mother cell into four equal portions. This type of tetrad division reminds us of the type of tetrad division of the tetraspores in Rhodophyceae.

No further description or discussion is given, and no figures of these stages appear in that paper. He does not state that a cell plate is absent, nor does he discuss the relation of the plasma membrane to the process. His statements given above, however, make it clear that he considers it a genuine furrowing and not simply a rounding up of the cells after division. Very recently Tahara (21) has published again on this subject, this time including six text figures of quadripartition in Chrysanthemum. These figures resemble very closely the figures which I published of Nicotiana (6), but he does not refer to any of my papers. He distinguishes three types

of tetrad formation, namely: the dicotyledonous type, the monocotyledonous type, and the rhodophyceous type. The last-named is obviously the quadripartition by furrowing, the monocotyledonous type is that of successive bipartition by cell plates, and the dicotyledonous type is apparently held to be quadripartition by cell plates, though he gives no forms in which such a process occurs nor does he refer to any papers presenting this type of division.

Gates and Rees (10) have just published their complete study of Lactuca in which they find quadripartition by furrowing, which they describe as exactly like that which I found in Nicotiana. They give five excellent figures of the stages of cytokinesis of the pollen mother cells.

Several Swedish investigators have been extending very rapidly our knowledge of the occurrence of quadripartition and successive bipartition respectively in the division of the pollen mother cells of monocotyledons. To the work of Täckholm and Söderberg (18, 19) have been added now two papers, one by Söderberg (17) and another by Palm (15) just last year. Söderberg (17) presents a list of more than 73 species of monocotyledons studied by himself and others. More than 38 have quadripartition, and more than 34 have successive bipartition. Quadripartition, he reports, is found in seven families of monocotyledons and successive partition in four. He himself in this paper reports the first case of quadripartition in a palm, namely *Chamaedorea corallina*. Palm (15) adds to the list of Söderberg observations on 8 additional families and on 19 species of families which have already been studied to some extent. It thus appears that up to the present successive bipartition and quadripartition have both been found in four families of monocotyledons; quadripartition alone has been found in six families; and bipartition alone has been reported in eighteen families. In the first group are the Naiadaceae, Liliaceae, Commelinaceae, and Orchidaceae. In the second group are the Juncaceae, Dioscoreaceae, Iridaceae, Taccaceae, Cyperaceae, and Palmae. Although Palm (15) does not take up a careful cytological study of the details of the process, he mentions a few observations which are in harmony with my findings. In the two species of Stemona in which he found successive bipartition he mentions that the mother cell walls are very thin. In Dianella, a lily, which has quadripartition, he reports that "no traces of a cell plate could be seen during the heterotypic division"; whereas in certain of the Amaryllidaceae having successive bipartition he reports that a conspicuous cell plate is usually present in the first division.

In 1907 Lubimenko and Maige (13) described the cytokinesis of the pollen mother cells of the two water lilies, *Nymphaea alba* and *Nuphar luteum*. In the former they found and figured the complete formation of a cell plate after the first division of the nucleus, though they state that it may never entirely extend to the plasma membrane on all sides. This cell plate disappears during interkinesis. In *Nuphar luteum* no cell plate

at all is developed after the heterotypic karyokinesis, though they report in extremely rare instances that a hyaline line may be seen across the equator. In *Nymphaea alba* they find a transitory cell plate appearing in the late anaphase of the homoeotypic mitosis, and their figure 51 substantiates this observation. No such transitory plate is found in *Nuphar luteum*. Their figures 53 and 52 show the tetranucleate stage of these two species respectively, with no partitions or cell plates present. Their figure 54 is of a pollen mother cell of *Nymphaea alba* after the partitions are completely formed separating the four cells. No further figures are given of cytokinesis. They describe the formation of the partitions as follows:

> Se forment brusquement les plaques cellulaires. Ce phénomène se produit très rapidement et on n'aperçoit, sur les coupes, que les plaques entièrement formées.

They interpret the disappearance of the transitory cell plate as due to the fact that the spindle fibers upon which it is formed are of nuclear origin, and that the material of which they are composed is used again in the formation of the linin thread and nucleoli of the new nuclei. The cell plate, which they believe is formed later and finally accomplishes division, is considered as being formed on spindle fibers of cytoplasmic origin appearing after the disappearance of the transitory cell plate.

Several considerations make it seem advisable to investigate further the cytokinesis of the pollen mother cells of some of the Nymphaeaceae. According to the work of Lubimenko and Maige (13), it would seem that *Nymphaea alba* resembles Magnolia in the existence of a transitory cell plate after the heterotypic nuclear division, but that it differs from Magnolia in that no incipient furrow is developed at this stage. *Nuphar luteum*, on the other hand, seems to correspond exactly to other flowering plants having quadripartition in so far as the events immediately following the first division of the nucleus are concerned. Furthermore, the instance of the disappearance of a transitory cell plate and the later formation of a permanent cell plate on the same spindle reported by these authors for Nymphaea apparently stands alone in the literature as the only case of such a behavior, and in itself would warrant further investigation.

For these reasons I collected pollen mother cells of *Nelumbo lutea* (Willd.) Pers. on July 9, 1921, at the Amana colonies in Iowa County, Iowa, where they grow luxuriantly in a large pond (text fig. 1). On this date large numbers of the flowers were in full bloom, but the blooming season extended on into August so that it is likely that the flowers used in this study would have bloomed in about mid-season. Reduction divisions occur in the pollen mother cells of this species when the buds are about one inch in diameter and about one and one half inches long. At this time the bud is between one and two feet above the water, the peduncle elongating only a few inches more before its growth ceases. In this, as well as in the forms which I have previously studied, it has been found that the stages of the

reduction divisions immediately precede the appearance of pigment in the anther, the yellow or orange tinge showing just after the microspores are formed. This fact aids much in readily finding the particular stages which are desired. After the examination of the pollen mother cells of one or

TEXT FIG. 1. The bed of *Nelumbo lutea* from which the material for this study was collected.

more stamens from a flower in living condition under a compound microscope in the field, other stamens from the same flower were fixed in Flemming's solution. In this way the desired stages were secured, and a large amount of imbedding, cutting, and staining in order to find the right stages was eliminated. The tip of the stamen projecting beyond the anthers, which is characteristic of this genus, was cut away before fixation in order to permit of ready penetration of the fixing solution into both ends of the stamens.

A longitudinal section of the stamen of *Nelumbo lutea* (Pl. XV, fig. 1) shows that the anthers are very long and slender. In most cases there is space for not more than four or five pollen mother cells to lie side by side across the pollen chamber in its widest place. During the reduction divisions the mother cells are usually not in contact with each other, but in

a region where there is room for four cells to lie side by side across the anther not more than three will be found. During presynapsis and the early stages of synapsis this large amount of intercellular space is filled with a colloidal matrix which disappears near the middle of the synaptic period and leaves the mother cells free within the anther during the remainder of the reduction divisions. Just after the disappearance of the colloidal matrix the mother-cell walls begin to thicken. Whether or not the material of the colloidal matrix contributes to the thickening of the wall, or whether the water released by dissociation of the intercellular colloid is subsequently adsorbed by the gelatinized cell wall of the mother cells, has not been determined. It may be that there is no relation between the disappearance of the gel between the cells and the thickening of the cell wall.

A peculiarity of the thickening of the walls of the mother cells of *Nelumbo lutea* is the high degree of inequality in the thickening on the various sides of the same cell. It is usually found that the sides of the cells toward the ends of the anthers are much more thickened than those toward the lateral surfaces. By the time the stage of interkinesis between the heterotypic and homoeotypic divisions is reached, it is found in some cases that the thickening of the wall on each of the two ends is equal to at least one half of the diameter of the cell lumen, whereas the walls on the lateral sides are scarcely thickened at all. Another feature noted about the anther of this species is that the tapetum usually remains living and intact throughout the reduction process. It consists commonly of very large cells, in some cases almost as large as the pollen mother cells. They may contain more than one nucleus, and mitotic figures are of common occurrence within them.

In Magnolia, as previously reported (7), the different stages of the reduction divisions may be found in the same anther, and there seemed to be no special arrangement or order of progression from one part of the anther to others. In Sisyrinchium (8), a very definite graded series exists from one end of the anther to the other. Either the distal or the proximal end of the anther may be more advanced, but there is a regular succession of stages, the whole range of stages in any anther not being very great. In *Nelumbo lutea* an intermediate condition exists. There is a succession of stages from one part of the anther to another, but it is not always from one end of the anther to the other. Furthermore, the range of stages found within a given anther is frequently much larger than in Sisyrinchium. Cases were found in which the tetranucleate condition was found at one end and the microspore stage at the other, with a series showing quadripartition in successive degrees of advancement between. In other cases diakinesis was found at one end of the pollen chamber and the tetranucleate condition at the other. In some cases both ends of the anther are more advanced than the middle. The middle portion may show interkinesis while the ends are in the tetranucleate stage; or the reverse may be true, with tetranucleate cells in the middle and interkinesis or even diakinesis at

both ends. It might be well at this place to explain the term "interkinesis," which I employed in my recent paper on Sisyrinchium (8) and am using again in the present paper. In 1912 Lundegårdh (14) introduced the term "interphase" to refer to the interval between two successive mitoses. He used it, however, in all cases to refer to the condition of the nucleus during that interval, making it coördinate with "prophase," "metaphase," etc. Sharp (16) in 1914 called attention to this meaning of the term, so that it now seems well established in cytological literature. It now appears that we need a term to refer to the condition of the entire cell between the time of the completion of cytokinesis and the initiation of the next succeeding karyokinesis. It is evident that the interphase condition of the nucleus may begin during cytokinesis, so that a new term coördinate with karyokinesis and cytokinesis is required, and "interkinesis" seems to be the logical choice. Throughout the study of *Nelumbo lutea* it was found that the karyokinetic stages in the reduction divisions seemed to be relatively few, whereas the cytokinetic and interkinetic stages were quite prevalent. This leads to the conclusion that karyokinesis proceeds in this form much more rapidly than cytokinesis, which hardly agrees with the findings of Lubimenko and Maige (13) in other species of this family.

The metaphase of the heterotypic division presents a very long spindle with a very narrow equatorial plate of chromosomes. The spindle is usually quite straight, though cases were noted where it curves gently at the poles. As nearly as could be determined the number of chromosomes is eight, though in some cases apparently good polar views revealed not more than five or six. This would of course be the gametophytic number. Apparently the number of chromosomes has never before been counted in this species. In 1898 Guignard reported 32 chromosomes in *Nymphaea alba*, and the following year Strasburger reported 48 for the same species. In 1897 Guignard reported 16 as the diploid number in *Nuphar luteum*, while Lubimenko and Maige in 1907 and Rosenberg in 1909 agree that the haploid number is 17.

The halves of the dyad chromosomes pull apart in the anaphases and pass to the poles in the usual manner. In the telophases the distance between the two plates of chromosomes is usually equal to or greater than the distance from either of these to the plasma membrane at its nearest point. Very soon after the chromosomes take this position the spindle fibers become apparently thicker along their middle portions. Whether this is due to a real thickening of the fibers themselves, or whether it is more or less of an illusion brought about by the crossing of fibers which lie nearly parallel to each other, is difficult to determine. But it soon becomes evident that a real thickening of the individual fibers has occurred, as there is formed a cell plate of these thickenings. These thickenings, which at first appear spaced, thicken until they touch each other, making a continuous layer. It does not extend beyond the limits of the central

spindle, however, and hence is to be considered as an incomplete cell plate. This incomplete cell plate may persist after the nuclei are completely reorganized, but it always disappears during early interkinesis at least. In no instance was a pollen mother cell in interkinesis or subsequent stages found in which complete bipartition had taken place.

Interkinesis is marked by the disappearance of the transitory cell plate and the subsequent enlargement of the two nuclei. The spindle fibers become progressively fewer and fewer, until in some cases it is practically impossible to find a single fiber connecting the two nuclei. The fibers are furthermore obscured by the formation of numerous large bodies in the cytoplasm during this period. These bodies approach the size of plastids, though they do not seem to have as definite boundaries as do those structures. They seem to be slightly flocculent in consistency, and it may be that further studies in chrondriosomes will reveal their nature.

The incomplete cell plate of Nelumbo seems to resemble that of Magnolia (7) to a considerable extent, except that it is perhaps somewhat more fully formed. Timberlake (23) reported such a structure as occasionally being found in the larch. He explains the failure to accomplish partition in these cases as due to a lack of formation of peripheral spindle fibers, and the same might be said of the condition in Nelumbo. Tangl (22) and Juel (11) found incomplete cell plates in Hemerocallis, but here they persist for some time after the telophases. A closer approach to the condition in Nelumbo is probably that reported by Juel (12) in Carex as occurring after both the heterotypic and the homoeotypic divisions.

The period of interkinesis is apparently quite long, and during this time the nuclei enlarge very much. They become very much larger than the nuclei which result from the second division, and can be easily distinguished from the latter by their size without consulting neighboring sections to determine the number of nuclei within the cell. These nuclei in interkinesis remain at some distance from the plasma membrane. No evidence at all of an incipient furrow such as was found in Magnolia (7) was revealed.

The homoeotypic mitosis is accomplished by the formation of long, narrow spindles which appear very much like those of the heterotypic mitosis except that they are smaller. In some cases the two spindles are almost exactly parallel, while in others they are almost exactly at right angles (Pl. XV, fig. 2). It seems likely that the usual condition is that the spindles are somewhere between parallel and at right angles to each other. At any rate, the division results usually in a tetrahedral arrangement of microspores, though there are some departures from this disposition.

Observations were made on many cells showing the homoeotypic telophase spindles at various stages, but in no case was a cell plate or orange zone seen. When the chromosomes first reached the poles, there was in one or two cases an apparent thickening of the spindle fibers throughout the middle portion of their length, just as was observed in the heterotypic

division. But in each case I was able to satisfy myself that this was simply due to the crossing of the fibers in this region. It is evident that if the halves of two homologous chromosomes lie side by side at the poles as they do in telophase, and if the halves of each pair are connected by spindle fibers, these fibers will cross and may even touch in the equatorial plane. In this case the appearance will be that of a much attenuated letter *X* with the upper and lower angles of the figure very small and the lateral angles very large. This is exactly the appearance which the equatorial plane of the central spindle in some of these cells presents. It is not followed by the obvious thickening of the fibers such as one finds in the heterotypic division, and consequently could not be taken as evidence of the development of a cell plate. Figure 2 is of a cell which is precisely at the stage when the early stages of cell-plate formation should be taking place, if they are to occur at all. It is at this stage of the first division that the transitory cell plate puts in its appearance, and in all other forms that I have studied the cell plate if it is formed at all is associated with this stage of the karyokinesis.

As the nuclei become organized they do not take the form of flat discs such as are found in Magnolia (7), but round up directly (fig. 3). As they round up and enlarge, the spindle fibers become fewer and fewer. No cases were found in which spindle fibers appear to be entirely lacking as in the stages of interkinesis, but they do become very scarce indeed. It is obvious that if a cell plate were being formed there would in all probability be a great increase in the number of spindle fibers especially in the peripheral region, but such is not found to be the case. The nuclei gradually migrate toward the plasma membrane as they enlarge, in a very similar manner to that found in Nicotiana (6). It must be that a relatively long period of time is involved in this stage of the formation of pollen. This is indicated by the frequency of these stages in the sections studied, and also by the enormous enlargement of the nuclei and their migration to the plasma membrane. An examination of figures 2, 3, and 4 suggests the degree of this enlargement. The volume of the nuclei shown in figure 4 is approximately four times that of the nuclei shown in figure 3. Furthermore, the cell itself has undergone an enlargement, that shown in figure 4 being about twice as large as that shown in figure 3. Even more marked than either of these changes is the enlargement of the nucleoli, which in the latter stage are many times their former size. The prochromosomes so distinct in the earlier stage are now quite indefinite in appearance. All the evidence seems to indicate that a long interval elapses between the completion of karyokinesis and the initiation of cytokinesis.

Following this, which is called the tetranucleate stage, there occurs the quadripartition of the cell by furrowing. This begins by the appearance of a structure which may at first seem to be a centripetally forming cell plate. A chip from the superficial portion of the protoplast may make it appear that there is a continuous plate across the equatorial plane. Such a

view is shown in the upper part of the cell of figure 4, where two spindles are crossed by continuous plates. That this is not a central section of the spindle but a superficial view is obvious from the fact that the upper nucleus does not appear in this section. But it is equally apparent that the appearance of the equator of the two upper spindles would be exactly the same in their central portion if the section had been cut so as to show a chip off the upper nucleus and similar chips off the two lower nuclei. Such a section would give evidence of a continuous plate across the central spindle, until a careful examination of adjacent sections showed this interpretation to be incorrect. It is doubtless this mistake which was made by Lubimenko and Maige and by other observers in reporting at least some of the instances of quadripartition by cell plates. A central section and careful focusing invariably, in all instances which I have seen, reveal the fact that this plate does not extend across the center of the spindle and that it is connected with the plasma membrane at its periphery.

From the time the furrow begins on the very boundary of the cell, there is an increase in the number of fibers of the central spindle. They seem to appear in centripetal order rather than centrifugally as in typical cell-plate formation. The furrow is very slender indeed, which adds to its resemblance to a cell plate as compared with the furrows of the other plants which I have studied. It is so thin, in fact, that it appears to consist during its development simply of the plasma membrane itself, and that cell-wall material is not found between the daughter cells until later. However, observation of cells which are somewhat plasmolyzed indicates that this interpretation is incorrect, and that a projection of the cell wall does extend into the furrow in some cases at least. Even at this stage of quadripartition the cell walls are usually not thickened to a marked degree on all sides. Figure 4 shows an enormous thickening of the wall above and a considerable thickening below, but the sides of the cell wall are rather thin. The middle lamella of the old mother cell is quite evident in some instances (fig. 4), while in other cases it seems to be lacking (figs. 2, 3).

A superficial view of the furrow indicates that it is perforated, as if it were made up of thickenings on spindle fibers as in typical cell-plate formation. Careful observation, however, reveals the fact that this perforated appearance obtains only on the inner margin of the centripetally forming furrow. Mrs. Farr (9) in her study of Cobaea found that the furrow as it advances inward presents not a simple cutting edge, but that its edge is wavy, the projections extending in between the fibers of the central spindle. Such a condition would give the appearance in section which is described above.

During quadripartition the furrows are apparently all simultaneously initiated within a given mother cell and proceed in their development at about the same rate, so that it is the portion of the central spindles between the exact central point and the exact center of the entire tetranucleate cell

which is the last to be traversed by the furrow. There are six spindles and four furrows as in Nicotiana (6), and the furrowing usually proceeds a little faster at the region of the junction of the three furrows, so that the furrowing may extend to the geometrical center of the cell before it has completely traversed the spindles. This situation was found in a considerable number of cells observed.

The mother-cell wall becomes more uniformly thickened on all sides as the microscope stage approaches. As noted above, the microspores when first formed are separated by very thin plates consisting of the two plasma membranes and a very thin layer of wall material. The spindle fibers are still quite conspicuous at this time, as was also noted by Lubimenko and Maige in the forms they studied (13). As the spindle fibers disappear the microspores slowly round up, the wall material becoming more abundant at the periphery at first. It is not clear whether this consists in the swelling of the material already in place or in the intrusion of additional material from the older portions of the surrounding wall. Although the rounding-up process takes place more slowly than in any form which I have previously studied, yet it is finally carried forward to the same extent as in the other forms.

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DESCRIPTION OF PLATE XV

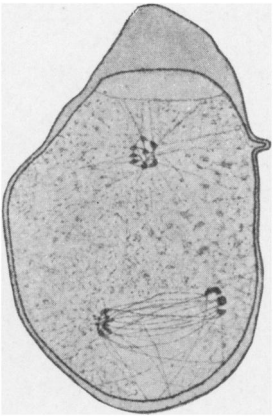
The photomicrograph was made with 1½ inch Professional Bausch and Lomb objective 24° and ocular 7.5 × with the plate at a distance of 42½ centimeters from the slide. The drawings were made after tracing the outline with a camera lucida. A Zeiss homogeneous immersion 2-mm. lens with aperture 1.30 was used with an 8 × ocular at a tube length of 145 mm.

FIG. 1. Photomicrograph of median longitudinal section of an anther of *Nelumbo lutea*, showing two pollen chambers with little more than a single row of pollen mother cells disposed freely within each pollen chamber.

FIG. 2. Pollen mother cell in a very late anaphase stage showing the lateral view of one spindle and a polar view of the other. Eight chromosomes may be counted. No evidence of a cell plate across the equator of the spindle is apparent.

FIG. 3. A tetranucleate stage in pollen formation. The nuclei have already enlarged somewhat. A cell plate, if present, should be well formed at this stage, but there is no indication of such a structure.

FIG. 4. A late stage of quadripartition by furrowing. The cytoplasm has become progressively more and more fibrillar, and the nuclei are larger. Note the relative thinness of the furrow and its uniform width. The unequal thickening of the mother-cell wall is well shown in this figure.



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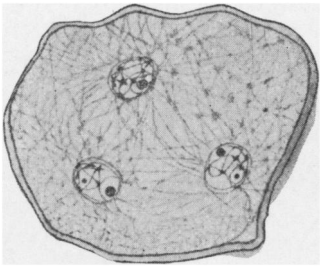

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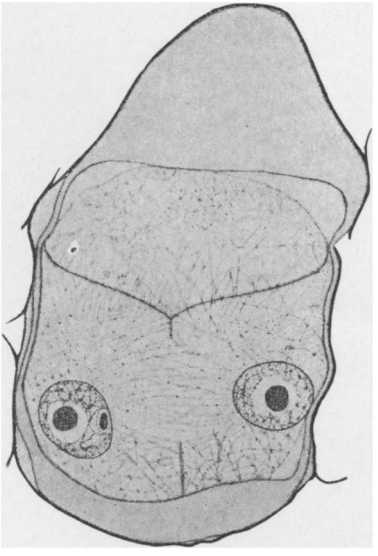

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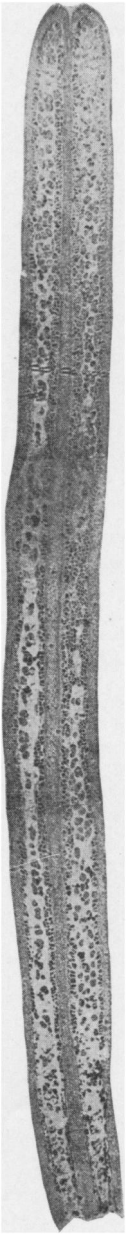

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FARR: CYTOKINESIS OF NELUMBO